

Observations on the Spawning Behavior and the Early Larval Development of the Sargassum Fish, *Histrio histrio* (Linnaeus)

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(Plates I-III)

INTRODUCTION

LITTLE is known of the spawning habits and larval development of pediculate fishes. The larval development of *Lophius piscatorius* Linnaeus has been studied more than that of the others (Proctor, 1928), but there is no report of either spawning behavior or larval development of any of the antennariids. It is a fairly common occurrence, however, for solitary sargassum fish, *Histrio histrio* (Linnaeus), in small aquaria, to produce rafts of unfertilized eggs very similar to those of *Lophius*. There has been no report of females having been paired, nor has any record been made of the collection of such rafts of eggs from the natural habitat in open water with a description of subsequent larval development, although the work of Proctor on *Lophius* employed such a naturally-occurring raft.

At one time there was confusion as to the identity of eggs thought to belong to *Histrio*, which were found in balls of sargassum weed, but Gudger (1937), in his historical survey, shows these to belong to flying fish and reviews the relatively numerous notes of egg rafts produced by *Histrio histrio* (*Pterophryne gibba*) in captivity. In the present paper, the taxonomic usage of Barbour (1942) has been followed.

It is well known that the sargassum fish is a voracious feeder and does not hesitate at cannibalism. Even with an adequate food supply present in a tank containing two or more sargassum fish, it is only a matter of a few days before only one will remain, the others having been eaten. Because of this cannibalism, individuals of this species are generally kept alone in aquaria. Thus, although there is no difficulty in obtaining eggs under laboratory conditions,

there is no record of pairing an ovulating female with a male.

In addition to the well-known egg rafts of the sargassum fish, Hornell (1921) reports that the closely related Indian species, *Antennarius hispidus* (Bloch & Schneider), occasionally spawned in the tanks at the Madras Aquarium, producing rafts of eggs very similar in his description to the egg mass of *Histrio histrio*. Here, too, however, the production of these egg rafts was by lone females and there is no record of fertilized eggs.

The studies here reported on both *Histrio histrio* (Linnaeus) and *Antennarius multiocellatus* (Cuvier & Valenciennes) were carried out at The Lerner Marine Laboratory, Bimini, Bahamas. My thanks are due Mr. Marshall Bishop, who succeeded in successfully pairing the fish and who made many helpful suggestions aiding in the raising of the young. Miss Priscilla Rasquin made careful observations of a second pair, independent of my records, and kindly submitted her data to me, greatly adding to an understanding of the typical behavior of these fish. I also wish to acknowledge the aid of Dr. C. M. Breder, Jr., in reading and criticizing the manuscript.

LABORATORY STUDIES

THE EGG RAFT

In his records of egg production by *Pterophryne* (*Histrio*), Gill (1908) defines the spawning period as extending from July through October. However, spawning activity does not seem to be confined to any one time of year. Breder (1949) reports an egg-laying schedule of one female which extended from March to the middle of May. The spawnings here re-

ported were observed from early January to the beginning of March. From these scattered records, no clearly defined spawning season is yet apparent.

The egg mass of *Histrio histrio* (Plate I, Figure 1) is transparent and glassy in appearance. When freshly spawned, it is very firm, having a distinctive form, and is about 3½ inches long without being spread out. This egg mass has been variously described as a band, raft or sheet of eggs. Its most distinctive feature when freshly spawned is the form of the two scrolled ends. From observation of the rafts spawned in captivity, it appears that the normal position of the raft is that of floating with the two ends rolling up and toward the middle of the raft, the left-hand scroll spiralling clockwise, the right-hand scroll spiralling counter-clockwise. There is no marked straight part of the raft between the two rolled ends; rather the band of eggs forms a broad smooth curve from one scrolled end to the other. The egg raft cannot be straightened out, as in unrolling a flat piece of paper, for the two edges curve slightly upwards at right angles to the length of the raft.

When samples of the egg raft are examined microscopically, it is apparent that the eggs lie in several layers throughout the mass and that each egg is separated from the others by a well-defined membrane, which appears to correspond closely to the true chorion found in perch eggs as discussed by Nelson (1953) and as described for *Perca americana* (Schranck) by Ryder (1887). As in the perch, the *Histrio* egg is free to rotate within the chorion, but there are no spaces between the membranes of adjacent eggs. The eggs in their membranes are tightly packed in the raft, the surfaces of the chorion pressed into irregular planes about the egg. In the four-day period of larval development before hatching, the firm framework formed throughout the egg mass by these chorionic membranes gradually becomes less sharply defined. As the membranes deteriorate, leaving only an incomplete mesh, the whole egg raft softens and swells to about three times its original size (Plate I, Figure 2). Although the raft is extremely buoyant when freshly spawned, it begins to sink slowly. Even at the time of hatching, however, the ends of the raft still maintain a modified scrolled form.

During the time at which the sargassum fish were exhibiting such great spawning activity, a small female *Antennarius multiocellatus* was kept alone in an aquarium. Over a period of several days this female swelled to enormous size (Plate I, Figure 3). She finally released an egg raft (Plate I, Figure 4) very similar to those of *Histrio histrio*. Following the produc-

tion of this egg raft, the *Antennarius* was once more reduced to very small size (Plate I, Figure 5).

The *Antennarius* egg raft showed scrolls at either end very similar to the distinctive form of the *Histrio* raft. In contrast to the *Histrio* egg mass, however, the middle of this raft appeared much longer and was relatively straight, not curving into the scrolls except at its extremities. Microscopically the structure of the raft is very similar to that of the *Histrio* raft, each egg being surrounded by a well defined membrane and the eggs in their membranes being tightly packed throughout the raft.

In his description of the structure of the *Lophius* egg mass, Proctor (1928) reports that "The embryos lie in a single layer in the mucus of the veil in capsule-like spaces containing from one to three or four eggs." These eggs were collected and first observed when they were beginning to form an embryonic shield. In the development of the *Histrio* egg, the breakdown of the chorionic membrane was, in one case, first noted just previous to the formation of the embryonic shield. It seems very possible that in the freshly spawned egg mass of *Lophius* there is a chorionic membrane encapsulating each egg, as was found to be true of the *Histrio*, and that by the time Proctor made his first observations of the *Lophius* veil, the firm membranes had begun to soften and become irregular.

COURTING AND SPAWNING BEHAVIOR

In all, five of the seven spawnings reported were closely watched from the first signs of courting behavior to the actual spawning. The spawnings watched all occurred in the late afternoon and early evening. The typical courting behavior became apparent in the early morning and continued through the day until spawning.

Egg Laying Cycle: First Female.—Two sargassum fish had been kept in laboratory aquaria for several months following their collection from floating weed. According to standard aquarium procedure in handling *Histrio*, as previously noted, each fish was in an individual tank. After several months in the laboratory, one of these fish produced an egg raft. On the same day, this known female was put into the tank in which the other *Histrio* had been kept. Up to this time, this second fish had produced no egg rafts in the laboratory aquarium, but there was no striking difference in the appearance of the two fish that would lead to identification of the male of the species. When the two fish were put together, neither one exhibited aggressive behavior towards the other. The second fish hovered close to the female constantly,

but made no attempt to attack or bite her. After three days together, the female produced another egg raft which was fertilized by the second fish. Following this, the pair spawned regularly every three days for more than two weeks. In all cases except the first egg raft production noted in the schedule below, the male was present and fertilized the eggs.

January 3rd, between 8:00 and 9:00 a.m.

January 6th, 4:35 p.m.

January 9th, 7:20 p.m.

January 12th, 8:35 p.m.

January 15th, 7:55 p.m.

January 18th, 7:15 p.m.

January 22nd, between 5:30 p.m. and midnight.

The egg masses were produced in very rapid succession and with a considerable amount of regularity, as may be seen by the above schedule. In a period of twenty days, seven egg masses were produced. Excepting the last spawning reported in the above schedule, there was a spawning every three days with a variation of only a few hours. Breder (1949) reported an egg-laying schedule for *Histrio* which included eight egg masses, the intervals between egg mass production varying from three to twelve days. This fish was a lone female and the eggs were not fertilized. The stimulation of the presence of the male may account for the rapid and regular production of eggs, three days, *i.e.* seventy-two hours, representing the minimal time for recovery from egg production and spawning to the maturation of the succeeding egg mass. The fish were not separated after each spawning, but left together in the same tank until after the fifth spawning, January 18th.

1st Spawning, January 6th.—The night previous to spawning, both fish of the pair exhibited normal tank behavior, hanging in the sargassum weed floating in the tank, drifting about and occasionally stalking and feeding on the live atherinids which were kept in the aquarium for that purpose. Although they did not show the actual courting behavior later found to be typical, the male maintained an attentive attitude towards the female, the two fish keeping close together most of the time. By early morning of the day of spawning, both fish showed marked changes in behavior. The female took up a position in a corner of the tank and did not move out from it at all throughout the day until the actual spawning. There was a shell to which a streamer of sargassum weed had been attached in the corner which the female adopted, and she spent the entire day holding onto the shell and weed with her pectorals, midway between the bottom of the tank and the surface of the water. In the early morning, about eight hours

before egg laying, the female showed some abdominal distention. This enlargement increased steadily throughout the day until spawning. In the early morning, the female maintained an almost horizontal position, but as the abdominal enlargement progressed, she gradually changed to an almost vertical position, snout tipped downwards (Plate II, Figure 1). Several hours before spawning the female exhibited very rapid and heavy respiration which lasted until after spawning. The female maintained a light yellowish tan color which closely matched the weed and is the typical color exhibited by sargassum fish kept in aquaria. Throughout the day, she kept her dorsal and caudal fins and first dorsal spines stiffly erected.

The male maintained a position close to the female, only once or twice during the day moving out from the corner. He was a much darker color than the female, almost a chocolate brown. The male kept both dorsal spines and dorsal fin tightly retracted to the body. He was much more restless than the female, circling her and nudging her with his snout, but never leaving her immediate vicinity. In the last few hours before spawning, the male became increasingly more active, moving constantly about the female, and occasionally nudging her with his snout and pushing at her with his pectoral fins.

Immediately previous to the spawning, the female moved out from her corner into the open part of the tank with the male following close behind. The female then began a march, head tipped down, appearing to walk across the sand bottom of the tank on her ventral fins. The male followed close behind, with his snout in immediate contact with the female's vent. In this manner the two fish marched back and forth the length of the tank about four times, the male maintaining his position relative to the female even when making sharp turns (Plate I, Figure 5). Then together they turned upwards, dashed to the surface, and the egg mass appeared to burst from the female. The time interval between the fish leaving the corner of the tank and the completion of the actual spawning was not more than two or three minutes. The spawning itself did not take more than a few seconds. Immediately after egg laying, the female appeared in an extremely exhausted condition. She was observed in disorganized spiraling about the tank, but during the following night both fish fed.

2nd Spawning, January 9th.—Previous to the second egg laying, the courting activity was similar, with little variation. The female occupied the same corner in the tank as before, maintained the typical light color, and kept dorsal and caudal fins well spread and dorsal spines

erected. Before spawning, the female did not exhibit the extremely rapid and heavy respiration shown previous to the first spawning, although respiration did increase to some extent. The male showed the distinctive chocolate brown coloration all through the courting period. He kept both dorsal spines depressed, but occasionally throughout the courting period he erected and depressed his dorsal fin. The male appeared more restless than in the first spawning, making short excursions across the tank and back, but his activity was always closely oriented to the female. The male exhibited increased activity as before just previous to spawning, pushing at the female with snout and pectorals.

This spawning followed much the same pattern as the previous one. The two fish came out of the corner together, the female appeared to walk across the sand on her ventral fins, snout down, with the male swimming in a horizontal position behind her with his snout closely applied to her vent. The fish made about five trips back and forth across the tank. During this march, the male kept his dorsal fin well spread. The female exhibited sporadic tremors. The male appeared to push the female ahead of him to within a few inches of the surface, then turned away and swam past her, breaking the surface as he passed above the female. This spawning was photographed at 64 frames/second. The motion pictures show the egg raft stretched from the female up to the surface of the water (Plate II, Figure 7). The count of the motion picture frames shows the contact of the male and female lasted only 0.4 seconds, from the time at which the two fish started from the bottom of the tank, dashed to the surface and the male passed the female and headed back to the bottom. The film shows that the female remained at the surface for an additional 2.5 seconds with the egg mass extruded but not completely detached from the vent, before shaking free of the egg raft and starting to return to the bottom of the tank. Immediately following this spawning, the male became much lighter in color, closely matching the female. The female did not exhibit the total exhaustion shown in the previous spawning, but settled to the bottom of the tank quietly, and within ten minutes after the spawning both male and female were stalking and feeding on the atherinids in the tank.

3rd Spawning, January 12th.—About twenty-four hours previous to this spawning, both fish fed extensively, together consuming at least ten atherinids. By early morning of the day of spawning, the female had once more settled down, occupying the same corner of the tank

as before. The male was even more restless than previously, making frequent trips back and forth across the tank, although these trips seemed oriented in relation to the female. Although the male made no attempt to feed on the atherinids present in the tank throughout the courting period, he exhibited aggressive activity towards foreign objects placed in the tank. If a hand was dipped into the water, he would dash at it vigorously.

About ten minutes previous to spawning, the male became very rough and aggressive towards the female, butting her forcibly with his snout and shoving her with his pectorals. The female appeared to make some attempt to avoid the male by pushing him away with her pectorals. Just before spawning, the two fish moved out of the corner of the tank together. The female did not settle to the bottom and march on her ventral fins as before, but swam slowly a few inches above the bottom, snout down. The male took up his typical position, swimming horizontally below and behind the female with his snout applied to her vent (Plate II, Figure 5). As the two fish swam slowly from one end of the tank to the other two or three times, the female exhibited the sporadic trembling which had been seen before. The egg raft appeared as the male pushed the female towards the surface (Plate II, Figure 6), but the female seemed to have difficulty in eliminating it, twisting and shaking herself at the surface. The male dashed quickly past the female, turning sharply away from her and swimming up, breaking the surface of the water. The actual contact of the two fish during this spawning was considerably longer than in the previously observed spawnings. The interval between the fish starting for the surface and the male heading back to the bottom was 2.8 seconds, this time being determined by a count of the motion picture frames covering the spawning. The female remained at the surface with the egg raft still streaming from the vent for an additional 6.6 seconds (Plate II, Figure 8). After the female had freed herself from the egg raft she appeared totally exhausted, having convulsions and spiralling about the tank for several minutes. Within half an hour, however, both male and female were quietly resting on the bottom (Plate II, Figure 9).

4th Spawning, January 15th.—The day previous to this spawning, the tank had been cleaned and the shell with its attached weed in one corner of the tank had been shifted slightly. In all previous spawnings, during the courting period the fish had hovered behind this shell and weed, which was the only protection available on the bottom of the tank.

In the morning before this fourth spawning, however, the female was in a position at the opposite end of the tank, braced with the aid of her pectoral fins between the standpipe and the end glass of the aquarium. However, to make photography possible the fish were disturbed and, with the aid of a glass plate, were crowded out of this end of the aquarium. They then immediately moved back into the corner with the shell and weed and hovered there, following the typical courting procedure. A few hours before spawning the male became excessively aggressive towards the female, shoving her with his snout and pectorals until finally, about a half hour before spawning, he appeared to force her from the courting corner out into the open part of the tank. As the male followed the female out of the corner, his color lightened from the typical chocolate brown of the courting period to a yellowish tan closely matching the color of the female. The male spread his dorsal and caudal fins extensively and periodically raised his dorsal spines. For the next thirty minutes the male persistently tried to get his snout near the female's vent in the typical position taken immediately before spawning, but the female pushed him away with her pectorals, at the same time slowly turning so that she faced him, then backed away slowly (Plate II, Figure 3). After thirty minutes the spawning occurred. Although not actually witnessed, the fish were heard splashing the surface of the water as they went to the top of the tank. The female showed no exhaustion immediately following the spawning and both fish fed within half an hour.

5th Spawning, January 18th.—The fish adopted the original corner of the tank behind the shell for the courting period. They exhibited the typical courting behavior, although the male appeared even more restless than before, continually making excursions across the tank and back. About an hour and a half before spawning the shell was moved out of the corner of the tank. The fish followed it out a way, then immediately returned to the corner. Twenty-five minutes before spawning, the male drove the female from the corner by forcibly butting and shoving her with his snout and pectorals. As the fish came out of the corner, the male lightened to a color matching the female. For the following twenty-five minutes the male alternately chased the female rapidly from one end of the tank to the other and sat quietly while the female rested. Several times during the chase, the male caught up with the female, took her entire caudal fin in his mouth and

gave her a very violent shaking (Plate II, Figure 4). At one time, he succeeded in catching the female by the anal fin and again shook her violently. No apparent damage was done to the female, but after a rapid chase and shaking the female was exhausted and would settle to the bottom. The male would leave the female for a few minutes and make several excursions across the tank, then return and start to nudge the female with his snout again. The female would fend him off with her pectorals, turning to face the male, until finally the male would force the female to swim ahead of him and once more begin to chase her. During this chasing the male became even lighter in color, almost pinkish.

After a short rest period, the female came up off the bottom slowly, the male came up behind her and put his snout close to her vent in the typical pre-spawning position. The fish swam slowly in this manner for not more than a minute, then started for the surface. As they started up, a bit of the jelly mass of the egg raft could be seen protruding from the female's vent. As the female reached the surface, the male turned away and swam up past her. The female remained at the surface for about a minute, shaking and twisting in an attempt to free herself from the egg raft. In this interval, instead of heading back to the bottom, the male made a short turn, coming up once more below and behind the female. From this position the male made another dash past the female as if fertilizing for the second time. The male then swam to the bottom, and the female settled down slowly with the egg raft still attached and apparently only about two-thirds eliminated. The female remained quiet several inches off the bottom with the egg raft streaming from her vent behind and above her. Her respiration was very heavy and rapid. The male came over slowly, approaching the female from below and behind. As his snout neared the female's vent, the male opened his mouth wide so that as he moved forward the egg raft lay across his jaws. He made no attempt to bite the egg raft but swam with it streaming across his jaws. As the egg raft came into contact with his jaws, the male turned away from the female and swam up past her, the egg raft running through his mouth. As the male swung away from the female, the egg raft was brought into position lengthwise under the body of the male. The male did not continue to the surface of the water but swam away from the female as the end of the egg raft passed through his mouth. The relative positions of the two fish and the path of the

male as he passed the female appeared identical to those observed in actual spawnings. Following this, the female appeared completely exhausted, and she slowly drifted over to a corner of the tank and settled down quietly with the egg mass streaming behind her. The male appeared to lose all interest in the female for several minutes. He changed to the typical yellowish color and started making frantic dashes across the tank. Shortly afterwards, the male quieted and approached the female again. He passed her, as described above, coming up behind the female and carrying the egg raft upwards across his jaws. Following this, the male once more became very active, dashing back and forth across the tank. The female moved slowly across the bottom of the tank, finally settling down in one corner. The male returned to the vicinity of the female and his behavior closely resembled that of the courting period. He turned a chocolate brown color, partially depressed his dorsal fin and moved slowly about the female. The female remained quite still, with her tail tipped up slightly, and the egg raft streaming above her. About three hours after the raft first appeared, the female suddenly shifted to a position on her side on the bottom. She remained in this position for almost fifteen minutes, while the male drifted attentively around and above her. Finally the female righted herself and rested quietly again a few inches off the bottom. Five hours after the first appearance of the egg raft, the fish still exhibited this courting behavior and the raft had apparently not been extruded to any greater extent. The following morning, ten hours after the initial effort, it was found that the female had succeeded in eliminating the egg mass. Both fish appeared normal and were near the surface of the water in the sargassum weed. The egg raft floated normally and there was no apparent difference in form between the scrolls at either end. Samples from either end of the egg raft were examined microscopically and it was found that, whereas eggs from the one end had reached a blastula stage normal for eggs twelve to fourteen hours after fertilization, the eggs sampled from the opposite end of the raft had not been fertilized, although they appeared fresh and normal. No motile sperm could be seen in these samples. Evidently the male did not fertilize the eggs when they were finally eliminated.

During the day following this fifth spawning, the male became increasingly aggressive towards the female, constantly chasing her about the tank. The fish were finally separated. The female was replaced in the male's tank

three days later and a spawning occurred. The male, however, exhibited extremely aggressive behavior. The female later died after being somewhat mutilated about her fins and tail by the male.

OBSERVATIONS ON ADDITIONAL SPAWNINGS

The month following the original spawning observations, a new female was placed in the tank with the male used in the original spawnings. The observations of these spawnings make an interesting supplement to those of the original pair. The production of egg masses was not as frequent as that of the first female; the courting period seemed in general to extend over a longer period than before; and the male did not exhibit the extremely rough behavior described above for the fifth spawning on January 18th.

Egg Laying Cycle: Second Female.—February 20th: An unfertilized egg raft was found in the morning in a tank with a single female.

February 25th, 9:20 p. m. Spawning.

March 3rd, 6:27 p. m. Spawning.

1st Spawning, February 25th.—Three days after the production of the first egg raft by this female, February 20th, the female was introduced to the male's tank. The male showed no aggression whatsoever, but became very attentive immediately. The male's jaw trembled conspicuously whenever he approached the female and occasionally tremors would go through his whole body. He hovered close to the female with all fins spread. The female appeared uninterested and kept her dorsal fin down because the male hovered so close above her. Occasionally the male brushed the female with pectoral and pelvic fins. Whenever the male left the side of the female, it was to swim back and forth displaying his fins. Except for these occasional excursions, the male remained in close contact with the female, his pectoral fins touching hers. Occasionally the male even got astride the female, settling down from above until he came to rest with his ventral fins spread across the female's back. The fish maintained this same behavior throughout the day, the female hanging in the weed and the male hovering about. Late in the afternoon the female was seen on the bottom of the tank, all fins collapsed, with the male on top in contact with her, also with all fins collapsed. The fish remained in this position with very little movement throughout the next two days until the early evening of February 25th. During the day of spawning the female appeared much enlarged, two swellings on either side extending from just behind the pectoral fins to the anus.

In the early evening, about an hour and a half before spawning, the male was observed pushing the female around the tank floor in front of him. The female was so large that she seemed unable to swim in proper balance. The male looked very much as though he were pushing a big ball with his nose. The male would occasionally nip the female in the stomach region. The male's fins were all erected, while the female kept her dorsal fin depressed. Occasionally the female would attempt to push the male away by pushing her pectoral fin against his snout. Several times the male opened his jaws very wide, then trembled afterwards. Occasionally he made a very quick, sharp movement, almost like an avoidance reaction. After a few minutes of rest, the male came up behind the female, appeared to bite at her, and forced her ahead of him out of a protecting shelter of algae-covered rock. He then again began pushing the female about the bottom of the tank, shuddering and butting the female out of corners, appearing to attempt to keep her up off the bottom. An hour before spawning, both fish appeared to be resting on the bottom once more, with all fins collapsed. They exhibited no further activity for at least a half hour. The actual spawning was not witnessed, but shortly afterwards both fish were removed from the spawning tank and they were separated from one another.

2nd Spawning, March 3rd.—The day following the first spawning male and female were put together again in the tank used previously. The male immediately began to hover close to the female, sporadically trembling all over in the same way as observed just before previous spawnings. In addition to this over-all trembling, the male exhibited occasional tremors of his lower jaw alone. The following day both fish remained quiet on the bottom of the tank, the male always in close attendance on the female. There was noticeable swelling again in the female's abdominal region. In the evening, the day before spawning, March 2nd, the female was observed holding herself with her pectoral fins in the weed at the surface with the male hovering underneath. The female's respiration appeared to have increased and her shape was changing; her anal fin appeared almost in the former position of the caudal, forced back by a large bulge above the anus. The skin appeared stretched tight and the female seemed to have difficulty in balancing herself. She released the weed which she had been grasping with one pectoral, but seemed unable to swim down, the caudal part of her body floating as if buoyed. The female was seen to give a wide yawn, sim-

ilar to those observed in the male. The male appeared very attentive, always hovering close to the female, usually with the top of his head in contact with her belly. Several times the female pushed him away with her pectoral. Occasionally the male gave a wide yawn.

In the early morning on the day of spawning, March 3rd, both fish were very quiet, the female being enlarged even more than previously noted. In the early afternoon, the female was on the bottom, with the male standing head down to one side with all of his fins spread over the top of the female. The two fish marched across the bottom, the female in the lead, the male pushing from behind. The male then stood once more on his head, bending the rest of his body over the female. The male showed a burnished copper color and kept his first dorsal spines stiffly erected, while the female's fins were all collapsed. The male swam at the female and then past her, after which she went to the surface and hung in the weed. The male hovered beneath the female, occasionally trembling. No dilation could be seen in the female's genital pore at this time. In his hovering, the male was in almost constant contact with the female's underside as she hung from the weed, occasionally leaning against her and trembling. The female's respiratory rate was almost double that of the male. The female gave a wide yawn, repeated by the male ten minutes later.

As the afternoon progressed, the male circled the female, in constant contact with her, trembling. He would yawn, then attempt to push the female down from the weed. He frequently brushed her ventral surface with his first dorsal spines. He gave a series of about fifteen yawns, then trembled repeatedly. The fish repeated these actions periodically until spawning.

The female remained just below the surface in the weed for about two hours until immediately before spawning. The male hovered very close, trembling and pushing at her with his pectoral and dorsal fins. During this period, the female showed little change except she had swelled even larger and appeared more nearly round, the anal fin forced into a caudal position, the caudal fin at an angle dorsally. The genital pore became visibly distended, although no papilla was evident. About an hour before spawning, distended and ruptured blood vessels could be seen in the tissue underlying the skin of the female's belly. The entire area of the female's body cavity posterior to the insertion of the pectoral fin was a bright, clear pink. Throughout this period, the male never ceased

pushing and shoving the female with fins and first dorsal spines. He repeatedly nudged the female's belly around the genital pore with his snout.

Two minutes before spawning, the female let go of the weed and the male immediately started shoving from behind, trying to start the march, but the female once again grasped a piece of weed with her pectoral. A minute later she released her hold on the weed and the male followed close behind, appearing to nibble at her belly. The two fish shot to the surface; the eggs were laid and fertilized. The actual spawning was so rapid that it was difficult to see what actually happened but it appeared that the eggs may have been slightly extruded and the male may have taken them in his mouth and with a sharp pull, extracted them.

Immediately after the spawning, both fish swam actively back and forth across the tank with all fins spread. The male appeared somewhat aggressive, but at no time during the courting period or spawning did he exhibit the extremely aggressive behavior observed in his spawnings with the first female. However, the two fish were left together after this spawning and the male became increasingly aggressive until several days later the female was found dead. She was in very bad condition, especially in the area of the caudal peduncle, which appeared to have been bitten repeatedly by the male.

DEVELOPMENT OF EGGS AND LARVAE

After every spawning the entire egg raft was removed from the aquarium. In several cases the jelly mass was cut into several pieces and each piece was set in a separate container with a supply of running sea water. The water temperature varied between 21° and 23° C. When the egg raft was cut, the larvae that broke out of the jelly mass hatched several hours earlier than if the raft was left whole. Small numbers of the larvae were put in large aquaria without running water. It was found that they could be kept successfully in this way for about six days, but at this time, when the yolk sac was almost used up, the larvae died.

Development Schedule:

0-2 hours: The egg is extremely transparent, glassy in appearance. It is oval when freshly laid and only becomes spherical at the time of the second cleavage (Plate III, Figures 1, 2). Before the first cleavage, the eggs average 0.7×0.6 mm. There is a fine line of lightly granular protoplasm encircling the yolk, concentrated at the

animal pole into a thin disc 0.3 mm. in depth.

2 hours: (Plate III, Figure 1). The first cleavage is complete, forming two equal blastomeres as a cap on the pole of the yolk.

3 hours: (Plate III, Figure 2). The second cleavage is complete, and the nuclei are distinct. The egg is now spherical.

4 hours: (Plate III, Figure 3). The third cleavage is complete, forming an eight-cell blastodisc. This blastodisc has spread out over the top of the yolk sphere, and some further cleavage lines may be indistinctly seen at its periphery.

5½-10 hours: There is a thin (probably one-cell thick) layer of cells spreading down over the yolk.

21-27 hours: (Plate III, Figure 4). The egg has reached a late blastula stage and a distinct germ ring can be seen.

27-36 hours: (Plate III, Figure 5). The entire germ ring has thickened considerably, one area expanded more extensively than the remainder, forming the beginning of the embryonic shield.

36-40 hours: (Plate III, Figure 6). The embryonic shield has thickened and lengthened very considerably.

40-48 hours: (Plate III, Figure 7). The neural keel is now apparent as a long band down the center of the embryonic shield. The average length of the embryonic shield at this time is 0.3 mm.

48-65 hours: (Plate III, Figure 8). The formation of the optic vesicle is first noted after the formation of three to four somites. The number of somites increases over a period of twenty-four hours. At the first appearance of the optic vesicle, the jelly mass of the egg raft has lost much of its rigidity, the entire mass softening and swelling and sinking to the bottom of the aquarium (Plate I, Figure 2). The microscopic framework of the jelly is breaking up, the regular octagonal capsule about each larva is becoming irregular and indistinct. The length of the three- to four-somite larvae is 0.5 mm.

65-75 hours: (Plate III, Figure 9). The somites now number thirteen to fifteen and the lens has formed in the optic vesicle. The head curves slightly ventrad around the yolk, the tail bud is free. There is a distinct enlargement dorsal and posterior to the head which appears to be the auditory placode. The total length of the larva is now 0.6 mm.

90-96 hours: Although still enmeshed in the soft jelly of the egg raft, the larvae are very active. The heart is beating strongly, and the tail, free of the yolk, twitches sporadically. Almost none of the capsule framework of the jelly mass remains.

4½ days: (Plate III, Figure 10). The newly hatched larva has a large yolk sac. There is considerable pigmentation; melanophores cover the top of the head and the eyeballs and there is a solid band of melanophores in the dorsal peritoneum across the top of the yolk sac. The pectoral fins are well developed but there is no evidence of the pelvic fins. The total length of the larva has reached 1.4 mm.

11 days: (Plate III, Figure 11). The yolk sac has almost disappeared. The gut has broken through to the exterior, caudad to the yolk sac. The larva is heavily pigmented both in the head region and in the dorsal part of the body cavity. One larva stained with toluidine blue shows that cartilaginous mouth parts are present at this stage. There is still no evidence of the appearance of the pelvic fins and there is no indication of the formation of any fins other than the pectorals. None of the larvae survived this age by more than a day.

RÉSUMÉ AND DISCUSSION

From observations described at length in the foregoing section, the generalized behavior patterns of these fishes during reproduction in small aquaria have been summarized below. Detailed description of each spawning was considered necessary to facilitate the emergence of a concept of the typical behavior pattern together with the range of variation that may be found within this pattern. Once the spawning activities of these fish are established, there is an adequate basis for comparison with the reproductive behavior of other pediculate fishes, of which there is yet no report.

In all the spawnings observed, although the fish fed the night before spawning, neither male nor female made any attempt to feed throughout the courting period which generally lasted about twelve hours. During the courting period, both fish remained mostly inactive, although at the approach of spawning the male became increasingly active, especially in the later spawnings with the first female. There was considerable variation in the colors exhibited by the fish during the spawning periods. Whereas in the first series the female retained the light tan color closely matching the sargassum weed, typical of these fish in captivity, the

male became a distinctive dark brown color during the courting period and kept it until the spawning occurred, when he resumed the light tan. However, the second female became almost as dark as the male did during the spawning periods.

Towards the end of the courting period, the typical position of the female was vertical, snout down. As the courting period progresses, the fish's abdomen swells and the center of gravity evidently shifts so that finally the female is standing on her head. The change of the center of gravity probably may be accounted for by the change of position of the eggs resulting from ovulation. The tremendous abdominal distention and the increasing buoyancy of the female previous to spawning seems to suggest that the egg raft may be almost in the same condition as when it is released. Moreover, there was no noticeable expansion or stiffening of the egg mass as it was released. Although it would be very unusual for the chorionic membranes to imbibe fluid while still in the body cavity, there seems to be sufficient indication that this may be the case to warrant further study.

After the extended courting period there is a very short pre-spawning march, during which the two fish position themselves for the amazingly rapid spawning. In the first two spawnings this march appeared definitely related to the bottom, but from observations on subsequent spawnings it is believed that this behavior was a result of the shallowness of the water. Typically, the female proceeds slowly, snout tipped down, with the male swimming in a horizontal position slightly below and behind her with his snout at the level of the female's vent. Then the female may swim to the surface with the male in position behind her, or she may be pushed upwards tail first by the male. In both cases, as the fish approach the surface, the male swings directly away from the female, swimming up past her, breaking the surface of the water, and returning to the bottom, leaving the female at the surface shaking free from the egg raft for several seconds. The duration of spawning is extremely brief, one spawning, which appeared slightly longer than others observed, lasting less than 10 seconds. It appears that as the fish go into the pre-spawning march, the egg raft is in its final form within the cavity of the female, permitting its very rapid release.

Although, because of the extreme speed at which the spawning takes place, it was impossible to see the precise behavior of the fish in the extrusion of the egg raft and fertilization, both direct observations and slow speed and single-

frame study of motion pictures of the spawnings point out the probable sequence of events. In all of the five spawnings of the first series, which were closely watched, the male's path past the female during the spawning appeared very similar, with little variation. From a position below and behind the female, with his snout just at the level of the oviduct pore, the male made a sharp turn of ninety degrees away from the female, and then as he gained a position out from under her, he turned to swim upwards past her. The male appeared to take almost the exact same path as he passed the female following the fifth spawning, which was incomplete, leaving the egg raft only partially extruded from the pore. The male followed the same path observed in the more normal spawnings, but very much more slowly. The manner in which the male turned away from the female with the egg raft in his mouth appeared to correspond closely to the movements in actual spawning. In the opinion of Miss Rasquin, from her observations on the second female, it appeared as though the egg raft might have been slightly extruded and the male have taken it in his mouth and, with a sharp pull, have extracted it. In the slow motion photography of the second spawning, although the detail is not clear, the frames covering the spawning show the female below the surface with the egg raft stretched from her oviduct pore upwards, where the male is splashing the surface (Plate II, Figure 7). Although the male cannot actually be seen, he has been traced to and from this position in the preceding and following frames of the film. It is possible that the egg raft, which is extremely buoyant, merely follows in the male's wake to the surface. However, the activity of the male observed in the fifth spawning of the first series points to the probability of the male taking an active part in stretching out the egg raft from the female's pore.

The successful mating of these fish without one eating the other may be attributed to pairing them when both were in full reproductive condition—which, to a great extent, was a matter of chance. These fish had been kept in individual tanks because of the cannibalism common in this species, and shortly before pairing both females had released egg rafts. Upon introduction of the female to the male's tank, the male displayed none of the aggressive activity usual towards any recent addition to the tank. The first female was left with the male even after spawning and the two lived successfully together. However, with each spawning the male became increasingly aggressive, although there was adequate food available, until the female finally died. The second female was removed

from the tank after her first spawning to avoid the aggression of the male, but after the second spawning the two fish were left together. The male did not show aggression during the pre-spawning period as with the first female, but after spawning he succeeded in killing the second female. In both cases, after the peak of spawning behavior, the male showed an increase of aggression, chasing and biting at the female, although he apparently made no actual attempt to eat her—which is typical behavior for any two of these fish in competition in one aquarium. The female apparently was in an exhausted condition after spawning and never exhibited aggression.

Comparison of the three available schedules of egg raft production, those of the two females reported here and the schedule reported by Breder (1949), suggests some stimulation of the female's egg production by the presence of the male. Intervals between egg production of the lone female reported by Breder range from three to twelve days. However, the first female reported here produced an egg raft regularly every three days over a surprisingly long period. This female was kept constantly with the male through the fifth spawning. At the time of the fifth spawning, the fish were separated for three days and the interval between raft productions was extended to four days. The second female here reported was separated from the male after her first spawning, although replaced with him after just one day. The interval between first and second spawnings here was six days. As this female was much slower than the first, when left with the male after spawning, the male lost his attentive courting attitude and became increasingly aggressive until the female was killed. The success of the long period of consecutive spawnings without separation of the first female was probably due to her ability to produce egg rafts in such rapid succession. Almost immediately after spawning, the male showed courting behavior. The schedule reported by Breder shows the female sargassum fish to be capable of short three-day intervals between egg mass production, but there was no male present and the intervals generally were much longer.

The development of the *Histrion* egg is relatively slow. When they are kept at a temperature varying from 21° to 23° C., the larvae hatch after four to five days. As development proceeds, the firm, gelatinous membranes of the egg raft deteriorate so that just before hatching the larvae are enmeshed in a loose framework which is all that remains of the chorionic membranes. For about six days following hatching the larvae drifted about the aquarium just be-

neath the surface film. The pectoral fins were well developed but the pelvic fins had not yet appeared. As with many of the pelagic fishes in captivity, none of the larvae survived after six or seven days following hatching, the time at which the yolk sac was used up and the larvae should have begun to feed.

The behavior pattern described for these fishes observed in aquaria must obviously be considered as modified from that occurring under natural conditions in beds of sargasso weed drifting in the open sea. Physical differences alone in the two environments would suggest modifications in the various phases of behavior. Normally only a single adult fish is found in one clump of weed, which circumstance can be related to the voracious appetite of *Histrio*. In this case, if they follow a pattern typical of many animals, it can be presumed that when the males reach the peak of sexual development they make expeditions into neighboring clumps of weed in search of a receptive female. On finding a gravid female, the courting behavior of the two fish would be substantially the same as observed in aquaria, including color change and relative quiescence until spawning. There are evidently no reports of the collection from one clump of weed of two fish, one differing markedly in color from the other. This question should be studied by means of field work.

The relative inactivity of the fish during courtship would be qualified by the constant motion of the sargasso weed in open sea. The male could be expected to move continuously, following the shifting position of the female. In deep water there would be no firmly anchored rocks or shells as on the bottom of the aquarium, but rather the lower mass of a weed clump. Under these conditions, it can be presumed that the well-defined pre-spawning march of these fish is considerably modified and probably consists only of the male shifting in the rolling weed until he can position himself for the dash to the surface with the female. Since there are such short intervals between these spawnings, it is probable that once the pair is established, the two fish remain together until one or the other is exhausted.

Although in aquaria the egg raft sinks to the bottom while the majority of the larvae still remain enmeshed in the partially deteriorated membranes, it is hardly conceivable that this should be the case in natural conditions. In the open sea even the mildest wave action would be expected to loosen the softened raft even further, allowing the larvae to break free while the raft was still at or just below the surface.

SUMMARY

1. From the spawnings here recorded and records in the literature of egg rafts produced by *Histrio histrio*, no specific spawning season has yet been defined.
2. The typical form of the egg raft produced by the sargassum fish is described.
3. An egg raft released by an *Antennarius multiocellatus* is described and compared with that of *Histrio*.
4. The microscopic structure of the egg rafts of both *Histrio* and *Antennarius* is described and compared to that of *Lophius piscatorius*.
5. The usual aggressive attitude of both sexes is evidently fully suppressed with the maturing of the gonads.
6. Schedules of the females' egg production are given, and courting and spawning behavior is described.
7. The progress of the *Histrio* egg and larva is described through eleven days of development.

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EXPLANATION OF THE PLATES

PLATE I. *Histrio* Egg Raft; *Antennarius* female and egg raft. All $\frac{1}{2}$ life size.

- FIG. 1. Fresh *Histrio* egg raft.
 FIG. 2. *Histrio* egg raft 3 days old. Sinking, swelling, and beginning to break up just prior to hatching.
 FIG. 3. *Antennarius* female with abdomen much enlarged just prior to elimination of egg raft.
 FIG. 4. *Antennarius* egg raft.
 FIG. 5. *Antennarius* female just following egg laying.

PLATE II. Courting Behavior.

- FIG. 1. Typical courting position: the female tipped snout down behind weeds with just the tail showing, the male hovering above her.
 FIG. 2. Typical pre-spawning position: the female below, the male above making a short turn without losing contact.
 FIG. 3. Advanced courting: the male on the left trying to force his way into position for the pre-spawning march, the female on the right pushing at the male with pectoral fin.
 FIG. 4. Extremely aggressive behavior of the male exhibited in the fifth spawning. The male on the left shaking the female by the tail.

Spawning Sequence from Selected Motion Picture Frames

- FIG. 5. Beginning of the pre-spawning march: the male below with snout closely applied to female's vent.
 FIG. 6. The male below pushing the female towards the surface with his snout.
 FIG. 7. Female below with the egg raft still attached stretched to the surface; the male splashing the surface.
 FIG. 8. Male on the bottom, female shaking free of the egg raft.
 FIG. 9. Male and female both on bottom, egg raft taking shape at the surface above them.

PLATE III. *Histrio* Eggs and Larvae. Photographed alive except 11-day larva. 42 \times except as otherwise noted.

- FIG. 1. 2 hours. 2-cell.
 FIG. 2. 3 hours. 4-cell.
 FIG. 3. 4 hours. 8-cell.
 FIG. 4. 21-27 hours. Early germ ring.
 FIG. 5. 27-36 hours. Beginning of embryonic shield.
 FIG. 6. 36-40 hours. Embryonic shield extended.
 FIG. 7. 40-48 hours. Late embryonic shield with neural keel.
 FIG. 8. 50-65 hours. 8 somites.
 FIG. 9. 65-75 hours. 13-15 somites, optic vesicle with lens, tail free.
 FIG. 10. 4 $\frac{1}{2}$ days. Large yolk sac, melanophores across top of yolk and in head region. 34 \times .
 FIG. 11. 11 days. Yolk sac much reduced, vent broken through, mouth parts formed. Stained and mounted. 34 \times .